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Quaternary paleoenvironmental variation and its impact on initial human dispersals into the Japanese Archipelago

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ABSTRACT

To understand the Late Pleistocene human dispersals to the Japanese Archipelago, we examine the paleobathymetric changes in and around the archipelago based on the results of recent paleoclimatological study of the Japan Sea that has provided millennium-scale sea level changes, the Pleistocene mammalian faunal record (e.g., extinct proboscideans), and the Paleolithic archaeological record. Proboscideans likely migrated from continental East Asia to Paleo-Honshu (consisting of the present day Honshu, Shikoku, and Kyushu islands) and the Ryukyu islands via land bridges across the Tsushima Strait and Yonaguni Strait during the coldest periods of the Middle Pleistocene (MIS 6, 12, 16, and probably 35). However, no clear evidence of hominin arrival in the archipelago has been dated to the Middle Pleistocene. Further, land bridges connecting continental East Asia and Paleo-Honshu were not present during the period of initial major human dispersals to the Japanese Archipelago, i.e., Marine Isotope Stage (MIS) 3 and 2. Thus, initial dispersals to Paleo-Honshu and the Ryukyus were achieved by watercraft and would have involved advanced seafaring skills. The paucity of archaeological sites before the onset of late MIS 3 (prior to 40 ka) and the significant increase of archaeological sites since late MIS 3 suggests that increasing population density on the East Asian mainland may have been a factor for humans to disperse into the Japanese Archipelago.

1. Introduction

Various behavioral traits have long been associated with modern humans (McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; d'Errico and Stringer, 2011; Shea, 2011). For instance, the ability to produce art and other forms of symbolic behavior (e.g., ochre, perforated ornaments) has traditionally been considered to fall specifically within the realm of modern humans and absent from other hominin taxa. However, the realization that at least in a few cases in Europe that Neanderthals may have produced evidence of symbolic behavior as well, has necessarily weakened this argument (Zilhão et al., 2010; Caron et al., 2011). Perhaps one of the few behavioral traits that has to this point, stood the test of time, is the ability to travel over large bodies of water via some type of watercraft to destinations that may not be visible from the points of departure. This trait has long been associated specifically with modern *Homo sapiens* (Davidson and Noble, 1992). The watercraft behavioral trait has long been part of the discussion for the earliest peopling of Australasia because most paleoanthropologists consider that only modern humans could have peopled the continent. Another region that may have only been peopled during the Pleistocene via watercraft and necessarily by modern humans is the Japanese archipelago (Norton and Jin, 2009; Norton et al., 2010; Kaifu et al., 2015; Bae, 2017; Bae et al., 2017; Nakazawa, 2017).

The Japanese Archipelago is a long chain of islands situated off the coast of the eastern Asian mainland (46° to 24° N, 123° to 146° E; Fig. 1). From north to south, it is comprised of Hokkaido, Honshu, Shikoku, Kyushu, and the Ryukyus. The northernmost island of Hokkaido is located from 46° to 42° N and it is separated from Sakhalin (Russia) to the north by the Soya Strait and Honshu to the south by the Tsugaru Strait. During glacial periods, Hokkaido and Sakhalin were connected to the mouth of the Amur River to form the Paleo-Sakhalin-Hokkaido-Kurile Peninsula (Paleo-SHK Peninsula), thus extending the eastern Siberian continent. Honshu is the largest island in the Japanese Archipelago, situated between 41° and 33° N and from 142° to 131° E. Honshu is separated from Kyushu to the south by the Kanmon Strait, which is very narrow, currently only 600 m wide, and from Shikoku by the Seto Inland Sea, a shallow sea that was dry during much of the Pleistocene. Kyushu is the largest island that lies closest to the Korean Peninsula, situated between 34° and 31° N. During glacial periods, Honshu, Shikoku, and Kyushu were joined together to form Paleo-

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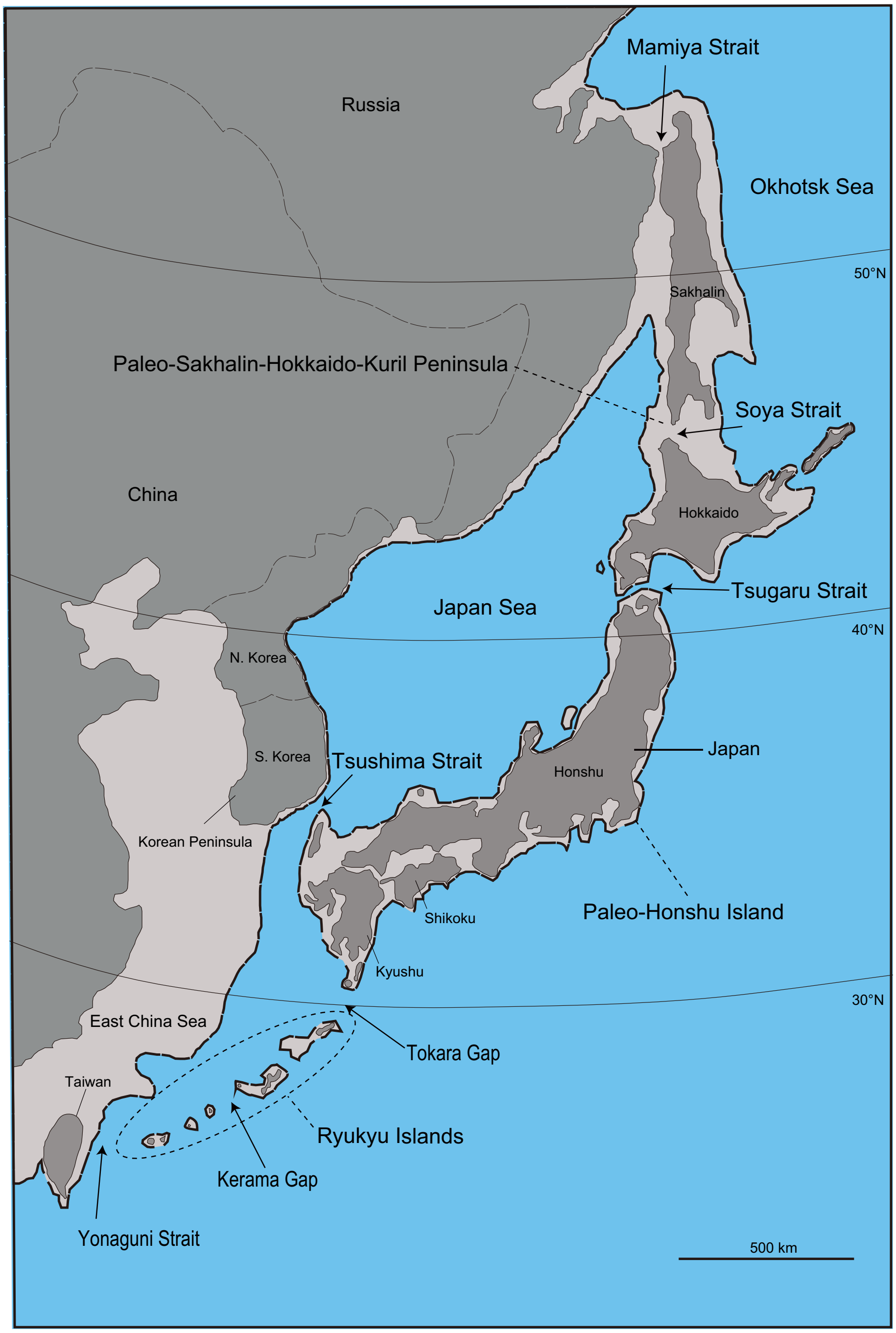

Fig. 1. General topographic map of the Late Pleistocene Japanese Archipelago and adjacent East Asia, consisting of the Paleo-Sakhalin-Hokkaido-Kuril Peninsula (Paleo-SHK), Paleo-Honshu Island, Ryukyu Islands, Taiwan, and Korean Peninsula. The bold line shows the coastal line along the bathymetry of 120 m below the present sea surface, drawn by referring maps in Japan Association for Quaternary Research (1987), Yonekura et al. (2001) and Iwase et al. (2012).

Honshu. The Ryukyus range from 31° to 24° N and are the southernmost islands consisting of the Osumi and Tokara Groups, Amami and Okinawa Groups, and Miyako and Yaeyama Groups from north to south. The Osumi and Tokara islands are separated by deep tectonic faults (~1000 m in depth), known as the Tokara Gap and the Okinawa and Miyako islands are separated by the Karama Gap (Konishi, 1965). Taiwan is located only about 100 km offshore of southern coastal China and about 110 km from the Yonaguni Island, the westernmost island of the Yaeyama Group in the Ryukus (Fig. 1).

During major glacial periods with lower sea levels, land connections were present between the mainland and the archipelago and directly relevant to discussions of the earliest peopling of the archipelago. Since the revelations concerning the Paleolithic hoax in Japan (Yamada, 2001; Nakazawa, 2010), the topic of the earliest peopling of the islands has taken on increased interest. Proponents of an early arrival by hominins to the archipelago suggest the peopling may have occurred some time during marine isotope stage ("MIS") 6 (191 ka–130 ka) when parts of the archipelago were likely connected to the Asian mainland (Matsufuji, 2010). The Sunabara site in western Honshu, that has been dated to MIS 5e, has been used as evidence to support this hypothesis (Matsufuji and Uemine, 2013; Uemine et al., 2016). The primary justification to support this argument are the observations of fractured surfaces on the recovered lithics from the alluvial sediments (Layer VIa), which are considered to be characteristic of purposeful knapping on rhyolite (Uemine, 2014). However, these "artifacts" are also associated with naturally fractured pebbles and debris (Matsufuji and Uemine, 2013); thus, further scrutiny of the site formation processes is critical (Nakazawa, 2017). Given the current situation that two small assemblages from a single site (i.e., Sunabara) are the only attributions to MIS 5e among the other possible "Early Paleolithic industry"

Table 1
List of possible "Early Paleolithic" sites in the Japanese Archipelago.

Regions	Sites	Chronometic dates	Stratigraphy with dated/datable tephra layers	Criterion to assign the site for the "Early Paleolithic"	Pros	Cons	References
Hokkaido	Rubenosawa	No	No	Lithic artifacts	Abundant lithic artifacts	No stratigraphic association with tephras and no chronometric dates	Takakura et al. (2001)
Honshu	Kanedori Cultural Level 3	68–35 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy and tephra deposits, amount of artifacts (n = 40)	–	Kuroda et al. (2005, 2016)
Honshu	Kanedori Cultural Level 4	68–85 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy and tephra deposits	Small number of artifacts (n = 8)	Kuroda et al. (2005, 2016)
Honshu	Kashiyamatate Layer 2c-lower	> 30 ka	Yes	Lithic artifacts and cultural level is below the AT tephra dated to 30 ka	Stratigraphy and tephra deposits	No chronometric dates from the cultural layer	Kikuchi (1996)
Honshu	Kashiyamatate Layer 4a	> 68–78 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	Small number of artifacts (n = 4)	Kikuchi (1996)
Honshu	Hoshino Tankenkan	No	No	Morphological traits of lithic artifacts	–	Surface collection	Sato (2016)
Honshu	Ishikobara	No	No	Lithic artifacts	–	No stratigraphic association with tephras and no chronometric dates	Nagano Prefectural Board of Education (1972)
Honshu	Takesa-nakahara	No	No	Morphological traits of lithic artifacts	Artifacts are from the Pleistocene loam	No stratigraphic association with tephras and no chronometric dates	Tsuruta (2010)
Honshu	Nutabura	No	Yes	Morphological traits of lithic artifacts	Stratigraphy	No chronometric dates from the cultural layer	Honkawane Board of Education (2003)
Honshu	Sunabara Cultural Level 1	120 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy and tephra deposits	Lithics are from alluvial and colluvial deposits with gravels, and number of artifacts is small (n = 6)	Matsufuji and Uemine (2013)
Honshu	Sunabara Cultural Level 2	110 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy and tephra deposits	Lithics are included in alluvial and colluvial deposits with gravels	Matsufuji and Uemine (2013)
Honshu	Kaseizawa		No	Morphological traits of lithic artifacts	–	Surface collection	Sato (2016)
Honshu	Fujiyama	No	No	Morphological traits of lithic artifacts	–	Surface collection	Sato (2016)
Honshu	Kiribara	No	No	Morphological traits of lithic artifacts	–	Surface collection	Sato (2016)
Honshu	Gongenyama 1	No	No	Morphological traits of lithic artifacts	–	Surface collection	Sato (2016)
Kyushu	Iriguchi Layer 4	103 ± 23 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	–	Hagiwara (2006)
Kyushu	Iriguchi Layer 3b	90 ± 11 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	–	Hagiwara (2006)
Kyushu	Ushiromuta Cultural Level 4	60–30 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	Small number of artifacts (n = 9)	Tachibana et al. (2002)
Kyushu	Ushiromuta Cultural Level 5	90–60 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	Little amount of formal lithic artifacts with abundant pebbles	Tachibana et al. (2002)
Kyushu	Kamishitada Level 5	No	No	Lithic artifacts	–	No stratigraphic association with tephras and no chronometric dates	Tachibana (1983)
Kyushu	Sozudai Level 5	110–50 ka	Yes	Lithic artifacts, site stratigraphy	Stratigraphy	OSL date for Level 5 is 27 ± 8 ka.	Yanagida and Ono (2007)
Kyushu	Ōno (the lowest cultural level)	> 30 ka, 79 ka (OSL)	Yes	Lithic artifacts, site stratigraphy	Stratigraphy and tephra deposits	–	Wada (2016)

(Table 1), the current data do not strongly support an MIS 6 hominin arrival to the archipelago.

These arguments for an early arrival aside, it is generally understood that the earliest human occupation of the Japanese Archipelago occurred some time during MIS 3 (e.g., Norton and Jin, 2009; Norton et al., 2010; Kudo and Kumon, 2013; Izuho and Kaifu, 2015). These dispersals to the archipelago originated from continental eastern Asia, and likely from the modern day regions of southern China, Korea, and/or eastern Siberia (e.g., Ohyi, 1968; Bae, 2017; Nakazawa, 2017). However, the nature of these Late Pleistocene dispersals is still poorly understood. We suggest that in order to be able to address this question about earliest human dispersals to the Japanese archipelago that paleoclimate, in concert with archaeological, data, must be more fully integrated into any early dispersal model. In particular, we need to more carefully evaluate the degree of paleobathymetric variation and how this influenced sill depths of the primary southern and northern straits (e.g., Tsushima and Tsugaru Straits) that currently separate the continent and the archipelago.

Pleistocene vertebrate fossils can also indirectly contribute to the earliest peopling of Japan discussion (Norton et al., 2010). For instance, a plethora of evidence indicates that various megafaunas like *Stegodon orientalis* and *Palaeoloxodon naumanni* arrived in the archipelago during MIS 16 and 12 respectively indicating clear land bridges between the Korean peninsula and Paleo-Honshu (Kawamura, 1998; Konishi and Yoshikawa, 1999). However, there is currently a complete absence of evidence of hominin occupation during MIS 16 and 12. Although this could change in the future, based on current research Middle Pleistocene hominins do not appear to have followed megafauna to the archipelago during these stadials. We focus the following discussion on three avenues of interest: 1) paleobathymetry; 2) vertebrate paleontology; 3) Paleolithic archaeology. Understanding these data in concert is critical to evaluating the earliest peopling of Japan question.

2. Paleobathymetry around the Japanese Archipelago

Although as many as six possible routes have been proposed for the earliest peopling of the Japanese Archipelago three paths seem to have at least some support: a southward route originating from continental Northeast Asia into Hokkaido; an eastward path from continental East Asia to Kyushu; and a northward route from continental Southeast Asia to the Ryukyus (Nakazawa, 2017; Fig. 1). The Sea of Japan forms a formidable barrier to many of these proposed dispersal routes to the archipelago, particularly because it has always been a large deep sea that was always filled with water; a situation quite unlike the nearby Yellow Sea that separates the eastern China seaboard and the Korean peninsula and would have been dry during glacial periods (Park, 2001; Norton, 2007; Bae and Bae, 2012). The Japan Sea is a semi-enclosed body of water situated in between the Korean Peninsula, a very small part of northern China, the Russian Far East, Sakhalin Island, and three major Japanese Islands (Hokkaido, Honshu, and Kyushu).

The Japan Sea is connected to the East China Sea to the southwest by the Tsushima Strait, to the northern Pacific to the east by the Tsugaru Strait, and to the Okhotsk Sea to the north via the Soya and Mamiya Straits (Fig. 1). Based on current sea levels (Table 2), all of these straits are narrower than 160 km (Gallagher et al., 2015). The depths of the Tsushima and Tsugaru Straights are relatively deep (~130 m), while those of the Mamiya and Soya Straits are much shallower (55 m and 60 m) (Ono, 1990; Oba and Irino, 2012). Because of their relatively shallow sill depths, the Mamiya and Soya Straits were likely land bridges during much of the Late Pleistocene. For example, the Soya Strait appears to be filled with water only during MIS 5e, 5c, 5a, and 1 (Ono, 1990). Because the maximum depths of both the Tsushima and Tsugaru Straights is ~130 m, debate exists about whether land bridges may have been present during glacial stages like MIS 4 and 2 (e.g., Ono, 1990; Park et al., 2000: Tada, 1995; Koizumi et al., 2006). These latter straits were clearly land bridges during major glacial periods like MIS 16, 12, and perhaps 6. Further, during glacial stages, the Ryukyus in southwestern Japan may have been connected to the island of Taiwan and subsequently to the Asian continent in Southeast China (e.g., Ujiié et al., 1991; Kimura, 1996; Ujiié, 1998; Ujiié and Ujiié, 1999). However, not all Quaternary scientists support this idea of a Pleistocene land bridge, because it is unlikely that subsidence during the last 20,000 years could have been rapid enough to create deep geological gaps such as the Tokara and Kerama Straights (Machida et al., 2001). Further, it has been suggested that this 20,000 year period was too short for indigenous plants and animals to have evolved in isolation on the Ryukyus (Kaito and Tada, 2016). Thus, the Ryukyus were likely separated from the Asian continent for a much longer time period.

Because the Tsushima and Tsugaru Straits are the likely routes by which humans arrived in Japan, the question of when they would have been dry has received a great deal of attention. Further, scientists have also been studying when the Ryukus may have been connected to the East Asian mainland by evaluating data from the Okinawa Trough. We evaluate these case studies in turn.

Data recorded in deep-sea sediments in the sampled piston cores from various locations in the Japan Sea have contributed tremendously to a better understanding of the paleoclimate and paleooceanography of Late Pleistocene Japan (e.g., Oba et al., 1991; Kido et al., 2007; Yokoyama et al., 2007; Ishihara et al., 2014). In particular, data derived from organic carbon, isotopic changes recorded in microfossils (e.g., planktonic foraminifera, radiolarian, diatoms, calcareous nannofossil assemblages), and concentrations of major elements have all contributed to estimate the millennium-scale variation in surface and deep water temperature and salinity of the Japan Sea (e.g., Oba et al., 1991; Keigwin and Gorbarenko, 1992; Tada et al., 1999; Kido et al., 2007; Yokoyama et al., 2007; Oba and Tanimura, 2012). In summarizing the various paleoceanographic studies of the Japan Sea, Tada and Irino (1994) distinguished four types of environmental proxies: (a) surface-water environmental proxy, (b) deep water oxic/anoxic proxy, (c) sea-level fluctuation proxy, and (d) loess fraction proxy. These data can contribute to understanding sea level changes and hence presence/absence of land bridges in Quaternary Japan. Both surface-water environmental proxy (a) and deep water oxic/anoxic proxy (b) provide variation in the forces of the Tsushima Warm Current, which in turn provides indirect evidence for sea-level changes. Land bridges would not only have turned the Sea of Japan into a very large deep lake, but some have proposed that the lower energy flow of the Tsushima Current caused the buildup of sands to bury the narrower Tsushima Strait (Oshima, 1980), and even that the northern half of the Japan sea may have been frozen during the Late Glacial (Suzuki, 1975). Sea-level fluctuation (c) is the most directly relevant data to determine presence/absence of land-bridge formations. The loess fraction (d) is an indirect measure as it provides data on relative dry/moist conditions that were cycled during the Late Pleistocene.

The surface-water environmental proxy (a) is the surface productivity measured by diatoms. For instance, a specific kind of diatom (*Paralia sulcata*) is found to only inhabit warm currents. An increase in this diatom reflects an increase in the influx of the Tsushima Warm Current that passes through the Tsushima Strait (Oba and Tanimura, 2012). The variability in the amount of diatoms in the Japan Sea is well correlated to the fluctuation in oxygen isotope ratios (Fig. 3 in Tada and Irino, 1994: their Fig. 3). The deep water oxic/anoxic parameter (b) represents the relative amount of oxygen in the deep water and this is related to deep-water convection and surface productivity (Tada and Irino, 1994). Depending on the degree of relative ratios of H_2S, the deep water conditions recorded in the sediments of the Japan Sea are distinguished into oxic, anoxic, and euxinic conditions (Tada et al., 1999). Tada and Irino (1994) found a correlation between the oxic/anoxic conditions in deep-sea water and fluctuations of sea-levels reconstructed from the oxygen isotope ratios. The deep water was euxinic during low sea-levels, corresponding to MIS 2, 6, 10, 12, 16,

Table 2
The straits around the Japanese Archipelago and their estimated depths and widths during the Last Glacial Maximum (LGM).

Straits/sea	Present sill depth (m)	Present width (km)	Estimated sea levels and land bridge emergence during the LGM		Methods	References
			Estimated sill depth (m)	Estimated width (km)		
Tsushima Strait	135	200	− 130 − 120 ± 7	20 20–30	^{14}C from continental shelves	Park et al. (2000) Oba and Irino (2012)
Tsugaru Strait	135	20	− 103 ± 12	1–2	Topography under the sea and hydroisostacy	Tada (1995); Matsui et al. (1998)
Soya Strait	15	40	0	Land bridge		Ono (1990)
Mamiya Strait	55	7.4	0	Land bridge		Ono (1990)
East China Sea: between China and Kyushu	200	700–800	− 120 ± 10	15 (to southern Kyushu)		Saito (1998)
East China Sea: between China and Ryukyu Islands	2270	400–500		200	Oxygen isotope ratios and ^{14}C	Saito (1998); Ujiié et al. (2003)
East China Sea: between China and Taiwan	100	130–200	− 120 ± 10	Land bridge		
Yonaguni Strait: between Taiwan and Ryukyu Islands	800[a]	110	NA	Land bridge?	Planktic delta ^{18}O values from cores of Okinawa Trough region	Ujiié and Ujiié (1999)

[a] There are different arguments regarding the land bridges between Taiwan and Ryukyu Islands. Please see the text.

presumably because deep-water convection that brought oxygen to the deeper levels of the Japan Sea stopped due to weaker or no intrusions of the Tsushima Warm Current (Tada, 1999; Tada and Irino, 1994; Tada et al., 1999).

Sea-level fluctuation of the Japan Sea (c) has also been estimated by the cyclic changes of paleobathymetry that are largely correlated to global changes in terrestrial ice volumes and regional tectonic uplift. Variations in terrestrial ice volumes are correlated to climatic conditions and well recorded in the oxygen isotope ratios (e.g., Chappell and Shackleton, 1986; Shackleton, 1987; Lambeck and Chappell, 2001; Siddall et al., 2003; Lambeck et al., 2014). The sea-level fluctuations in the Japan Sea have been estimated by the oxygen isotope ratios of sediment cores (e.g., Oba et al., 1991; Oba and Irino, 2012), as well as the ^{14}C dates of fossil shells from the Tsushima Strait (Park et al., 2000). Sea levels have been mainly constrained by eustatic changes due to global climate changes (e.g., Lambeck and Chappell, 2001; Siddall et al., 2003; Yokoyama et al., 2007). Overall, estimates place the sea level drop during glacial stages in the Tsushima Strait to between 120 and 130 m, indicating that the region would have been dry land (Table 2. Despite the deep sea sill depth of the Tsugaru Strait (− 130 m) that is almost identical to that of the Tsushima Strait, the issue of whether a land bridge across the Tsugaru Strait was present or not has received much less attention than the Tsushima Strait. At least part of the reason for the paucity of attention on the Tsugaru Strait is that many studies have shown that sampling from the Tsushima Strait can provide robust evidence of the salinity and intensity of the Tsushima Current into the Sea of Japan and in turn this can be related to the varying width and depth of the Tsushima Strait (e.g., Tada et al., 1999; Yokoyama et al., 2007).

Considering the hydroisostacy (Nakada et al., 1991, see also Okuno et al., 2014), Tada (1995) estimated that the uplift of oceanic crust under the Tsugaru Strait was 9–23 m, while that of the Tsushima Strait was 0–3 m. Given these local tectonic uplifts, sea level of the Tsushima Strait dropped 117 ± 5 m during the Last Glacial Maximum. However, because the Tsugaru Strait has a 130 m sill depth, a land bridge across the Tsugaru Strait that connected Hokkaido and northern Honshu would not have formed even during the Last Glacial Maximum (Tada, 1999). Further, as shown in Fig. 2, the Tsugaru Strait has a series of deep ocean basins (− 150–200 m) including the Tsugaru, Tayama, and Matsumae Ocean Basins (Oshima, 1980) that would have still been present even at the peak of these glacial periods (Tada, 1999; Matsui et al., 1998).

While a similar situation is found in the East China Sea and the Ryukyus, the Late Pleistocene paleogeography in and around the Ryukyus is more complex than Tsushima and/or Tsugaru. A deep back-arc basin called the Okinawa Trough (Lee et al., 1980; Kimura, 1985) lies in the northwestern area of the Ryukyus that reaches depths of 2000 m. It is clear that even during major glacial periods no land bridges would have been present (Saito, 1998). Although no land connections existed, a decrease of 120 m in sea level depth would still have resulted in a substantial expansion of a previously submerged shelf that extended from 25° N to 23° N and from 120° E to 125° E (Saito et al., 1998; Kao et al., 2008). The paleoshoreline would run nearly parallel to and much closer to the Ryukyus (Fig. 1).

Regarding possible land bridges between southern China and the Ryukyus much debate exists, particularly about the possibility that Taiwan and the Ryukyus may have been connected during the Late Pleistocene (e.g., Kizaki and Oshiro, 1980; Kimura, 1996; Ujiié et al., 1991, 2003; Ota, 1998). This proposed land bridge, referred to as the "Ryukyu-Taiwan land bridge" (Ujiié and Ujiié, 1999: 23), was identified by oxygen isotope ratios and frequencies of planktonic foraminifera from piston cores in and around the Ryukyu Islands (Table 2). The "Ryukyu-Taiwan land bridge" that emerged during the LGM eventually disappeared due to tectonic activities about 10,000 years BP that served to create the present day deep sill of 800 m in the Yonaguni Strait lying between Taiwan and the westernmost Ryukyu island of Yonaguni (Ujiié et al., 2003). Nevertheless, this model has been criticized by several vertebrate paleontological studies (e.g., Ota, 1998; Nishioka et al., 2016). For example, based on the geographic distribution of various Late Pleistocene reptiles on the Asian mainland and the Ryukus, Ota (1998) argued a land bridge was never present. The appearance of megafauna on the islands does suggest at least that the Ryukus were connected some time during the late Middle Pleistocene (Kawamura et al., 2016) (Table 4).

3. Estimations of Pleistocene land bridge(s) inferred from vertebrate faunas

The first appearing datums of vertebrate faunas in the Japanese archipelago that clearly originated from the Asian mainland can provide evidence of when land bridges existed during the Pleistocene (Kawamura, 1991; Konishi and Yoshikawa, 1999; Kuzmin et al., 2000; Takahashi et al., 2006; O'Regan et al., 2011; Suzuki et al., 2015; Kaito and Tada, 2016; Kawamura et al., 2016). Four megafaunal taxa (*Mammuthus trogontherii*, *Stegodon orientalis*, *Palaeoloxodon naumanni*, and *Mammuthus primigenius*) have received the most attention regarding

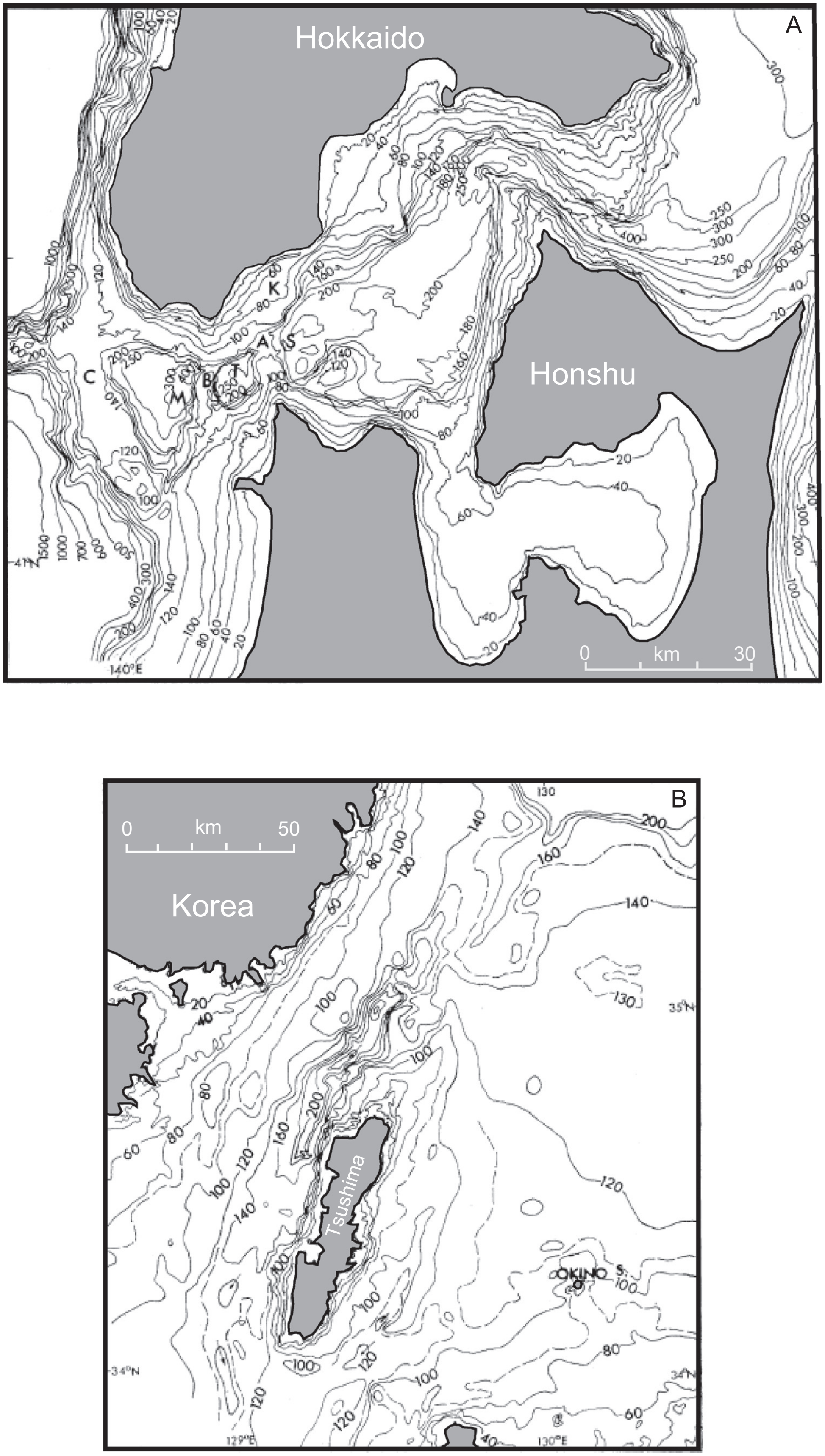

Fig. 2. Bathymetric chart of the straits compared between (A) Tsugaru Strait and (B) Tsushima Strait. Original maps are adopted from Oshima (1980).

Table 3
First appearances of Proboscidean and *H. sapiens* in the Late Pleistocene Japanese Archipelago.

Taxon	The oldest fossil record				Inferred timing of the emergence of land bridges
	Paleo-Honshu	Paleo-SHK	Ryukyu	Estimated survival duration	
Mammuthus trogontherii	1.2 Ma	–	–	MIS 35–15	0.2–0.7 Ma (Taruno and Kawamura, 2010)
Stegodon orientalis	0.6 Ma	–	–	MIS 16–12	MIS 16 (Konishi and Yoshikawa, 1999)
Palaeoloxodon naumanni	0.34 Ma	30,520 ± 220 years BP[a]	–	MIS 10–2 (MIS 12[b]–2)	MIS 12 over the Tsushima Strait (Konishi and Yoshikawa, 1999)[b]
Mammuthus primigenius	–	45,110 ± 480 years BP[a]	–	MIS 3–2	MIS 3–MIS 2 and before over the Mamiya and Soyo Straits (Ono, 1990)
Homo sapiens	MIS 3[c]	MIS 2[c]	MIS 3[d]	–	–

[a] The date is from Takahashi et al. (2006).
[b] Konishi and Yoshikawa (1999) estimated the initial dispersal to the Paleo-Honshu was in MIS 12 crossing presumed land bridge on the Tsugaru Strait.
[c] Evidence based on archaeological record from the Nekata site at Hamakita (Kondo and Matsu'ura, 2005).
[d] Evidence based on human paleontological record from the Yamashita-cho (Suzuki, 1983).

these Quaternary land bridges (Kawamura, 1998; Konishi and Yoshikawa, 1999; Norton et al., 2010). Table 3 summarizes the estimated arrival of and survival duration for these proboscideans in the Japanese Archipelago. The first Proboscidean to arrive in the archipelago was *Mammuthus trogontherii*, estimated to have arrived around 1.2 Ma and was present until ca. 0.7 Ma based on specimens from various locations in the Japanese Archipelago except Hokkaido (Taruno and Kawamura, 2010). This wide age range is based on the estimated age of the Osaka Group, a series of Pliocene to Middle Pleistocene sediments distributed in and around the Osaka Plain in western Honshu (Yoshikawa, 1973; Taruno and Kawamura, 2010). The proposed Middle Pleistocene land connection between southern China and the Ryukus is based on the presence of an M3 identified as *M. trogontherii* from Miyako Island in the southern Ryukyus (Taruno and Kawamura, 2010). *Stegodon orientalis* was discovered in the upper layers of the Osaka Group. Given the position in the upper layers, *S. orientalis* is thought to date to MIS 16 (~0.6 Ma) which was a major glacial stage when a land bridge would have been present (Konishi and Yoshikawa, 1999; Yoshikawa et al., 2007; Taruno, 2010).

While *Palaeoloxodon naumanni* was found in the Osaka Group dated to 0.34 Ma (MIS 10), the arrival of this taxon is estimated to be MIS 12 when sea levels were low enough for a land bridge to develop across the Tsushima Strait (Konishi and Yoshikawa, 1999). However, given the fact that most *P. naumanni* fossils found in China are in deposits younger than MIS 10, their dispersal from the continent to the archipelago may well have occurred during MIS 10 given *P. naumanni*'s ability to swim (Kondo, 2011; Takahashi, 2011). *Palaeoloxodon naumanni* disappear from the Japanese record during MIS 2 based on a critical examination of associated ^{14}C dates (Iwase et al., 2012). It has been suggested that *P. naumanni* may have swam across the Tsugaru Strait during MIS 3 to arrive in Hokkaido (Takahashi et al., 2006). However, this dispersal northward is considered to have been only a minor excursion given the absence of a land bridge between Honshu and Hokkaido (Takahashi, 2011).

Mammuthus primigenius is the last of the four major megafauna to appear in Japan. All *M. primigenius* fossils (teeth) except one are from Hokkaido and date to between 45 ka and 20 ka based on 11 radiocarbon dates from 11 specimens (Takahashi et al., 2006). The vegetation in Hokkaido during 60 ka–35 ka and 25 ka–10 ka was open taiga forest comprised of *Larix gmelinii*, *Picea pumila*, and *Picea jezoensis*, along with grassy plains (Igarashi et al., 1993). This grassy plain is often referred to as 'mammoth steppe' (Guthrie, 1990); an environment that would have facilitated *M. primigenius* dispersal in the Paleo-SHK peninsula and adjacent northerly regions in Beringia during MIS 3 and early MIS 2 (Takahashi et al., 2006; Macdonald et al., 2012). During the LGM, this open forest environment transitioned to a more deciduous broad-leaf forest, which may have prompted *M. primigenius* to migrate north out of Hokkaido through the land bridges over the Soya and Mamiya Straits and back to Siberia (Iwase et al., 2012). It may be possible that the late arrival of humans in the region may have impacted *M. primigenius*' presence in Hokkaido, though interdisciplinary studies are clearly needed to investigate this possibility further.

Several different models have been proposed to explain the local extinction of these various megafaunas in Japan, models that lean in one direction toward climatic changes (Takahashi and Izuho, 2012; Iwase et al., 2015) and in the other direction on human influences (Kawamura, 2007; Norton et al., 2010; Bae, 2017). Although not many researchers support a single cause explanation for the extinction of megafaunas on the archipelago during MIS 2, the role of humans in these extinction scenarios has tended to be minimized or excluded entirely (e.g., Iwase et al., 2015). However, given the fact that Paleolithic occupations on the archipelago exploded after 30 ka (going from tens of sites to thousands of sites) would suggest that expanding human home ranges played at least an indirect role in forcing these megafaunas to less hospitable environs and eventual extinction (Bae, 2017). What is clearly needed in Japanese Paleolithic research is more detailed taphonomic studies that are designed to distinguish between natural and hominin-induced deaths and accumulations of these various Pleistocene faunas (e.g., Norton et al., 2007, 2010). Only then will it become clearer the role, if any, of human foragers in the extinction of various faunas in the archipelago during MIS 3–2.

A taxon that has not received as much attention in discussions of paleo-land bridges in Japan is the non-human primate *Macaca fuscata*, which is clearly not indigenous to the islands. Macaques are currently present in several different regions on Honshu, but were more widely spread during the Pleistocene. Based on current data, macaque fossils were identified in association with *P. naumanni* fossils in the Yurimizu Quarry suggesting that the two may have dispersed during MIS 12 (Iwamoto and Hasegawa, 1972; Aimi, 2002). It may be possible that macaques though arrived much later during MIS 6 when the last clear land bridge would have existed. Interestingly, when humans arrived on the islands, the megafaunas mostly disappeared, while macaques continued into the present day. Perhaps the latter's ability to follow a more generalist diet and breed at higher rates facilitated their survival into the present day (Jablonski et al., 2000).

4. Human dispersals into the Japanese Archipelago

Humans could have arrived in Japan during the Pleistocene one of two ways: via a land bridge or watercraft. Land bridges were present during the Middle Pleistocene during MIS 16, 12, and 6, but there is currently an absence of evidence of a hominin occupation of the islands during any of these glacial stages. The question then becomes, did the absence of land bridges constrain human dispersals into the Japanese Archipelago? In other words, would the presence of land bridges accelerate hominin dispersals from the continent to the archipelago? Data from Korea may be able to contribute to answering these questions. Although the Komunmoru Cave site in North Korea is coeval with

Table 4
Presence and absence of archaeological occupations in Middle and Late Pleistocene Japan.

Climatic periods		Estimated land bridges					Archaeological record		
	Number in figure	1	2	3	4	5	Regions		
	Duration (years BP)	Mamiya Strait	Soya Strait	Tsugaru Strait	Tsushima Strait	Yonaguni Strait	Paleo-SHK	Paleo-Honshu	Ryukyu
MIS 2	30,000–11,500	■	■				■	■	■
Late MIS 3	40,000–30,000	■	■					■	
Early MIS 3	59,000–40,000	■	■					1	
MIS 4	71,000–59,000	■	■						
MIS 5a–5d	114,000–71,000							6	
MIS 5e	128,000–114,000							2	
MIS 12	435,000–429,000				■				
MIS 16	670,000–640,000				■				

Black blocks have a reliably dated archaeological record and a presence of land bridges. Gray blocks have a tentatively attributed archaeological record, while questions exist about the associated dates.

Zhoukoudian Locality 13 and may date to c. 1 Ma, the relationship between the paleontology and purported artifacts is not clear. The next set of potential early occupations of the Korean Peninsula date to the Middle Pleistocene at Kumgul and some of the sites located in the Imjin-Hantan River Basins (Norton, 2000; Norton et al., 2006; Norton and Bae, 2009; Bae et al., 2012; Bae, 2014). However, prior to the advent of the Late Pleistocene, relatively few archaeological sites have been identified. Thus, if the Korean Peninsula was not very densely populated by hominins until the latter half of the Middle Pleistocene it is perhaps not all that surprising that hominins are also absent in the Japanese Archipelago during MIS 16, 12, and perhaps even 6 (Table 4).

The earliest purported sites in Japan tentatively have been dated to MIS 5 (Table 4). In Table 4, the black regions indicate when clear evidence of human occupation is present in which region and the gray areas, with the number of sites for each time period, represent possible early arrivals of humans (Kuroda et al., 2016; Sato, 2016; Uemine et al., 2016; Wada, 2016). The total number of sites in the gray area is nine, but originally was 20. Based strictly on techno-typological traits, Sato (2016) assigned a total of 20 lithic assemblages and groups of surface-collected artifacts into a so-called “Early and Middle Paleolithic” industry. The stone tool classes of the “Early and Middle Paleolithic” lithics are mainly choppers, chopping tools, and amorphous flakes with/without retouch and crude cores (Kuroda et al., 2016; Tachibana et al., 2002), and their characteristics are quite different from those of the assemblages dated to the late MIS 3, which are best represented by trapezoids, edge-ground handaxes, and knife-shaped tools.

Despite this typo-technological variation, the chronometric dates for at least some of the “Early and Middle Paleolithic” assemblages are not reliable, given that their stratigraphic relationship to datable layers (e.g., tephra units) underneath and above the cultural levels is questionable. In fact, only a few of these lithic collections originate from secure stratigraphic contexts, such as Kanedori IV and Kanedori III (Kuroda et al., 2016) (Table 1). Eliminating imprecisely dated cultural levels and surface collected artifacts that have no known ages, the 20 “Early and Middle Paleolithic” assemblages identified by Sato (2016) can be reduced to nine (Table 1, Table 4). The majority date to early MIS 3, though some assemblages such as Sunabara (Matsufuji and Uemine, 2013; Uemine et al., 2016) have been assigned to MIS 5e. Of these 9 sites, Kanedori III (Kuroda et al., 2016) and Ōno (Wada, 2016) appear to be the most reliable. Given the fact that the last Pleistocene land bridge likely dates to MIS 6, even if all of these lithic assemblages stand up to further scientific scrutiny, hominin dispersals from the mainland over a land bridge was likely very infrequent. It is not until MIS 3, particularly beginning during late MIS 3 (40,000–30,000 years ago), where human arrival on the islands became more pronounced. Apparently, the Tsushima Strait did not serve as a physical barrier for human dispersals during late MIS 3, but clearly watercraft and great seafaring skill was involved.

Reasons need to be explored for why human foragers decided to build watercraft, develop seafaring skills, and explore new regions during MIS 3 that for all intents and purposes were considered completely unknown. The push and pull model to explain mammalian dispersals in paleobiology (Anthony, 1990; Clark, 1994) could provide the ecological justification for what prompted Late Pleistocene human foraging groups to disperse to new territories. The push factors potentially include stress in the homeland such as population growth and resource depression and the pull factors include lower population densities and greater resource abundance than the homeland (Clark, 1994). During the Pleistocene, these changes in human population and resource abundance are likely in part related to climatic fluctuations.

In applying the push and pull model to Pleistocene human dispersals into the Japanese Archipelago, the questions would be what were the “push” factors in the continent and what were the “pull” factors in the archipelago? Data from various disciplines indicate that the climate during late MIS 3 was generally cool in Paleo-Honshu and Paleo-SHK, while the millennium-scale climatic changes represented by the Dansgaard-Oeschger cycles during MIS 3 did not cause major changes in biomes (Takahara and Kitagawa, 2000; Igarashi and Oba, 2006; Kumon et al., 2009; Hayashi et al., 2009; Takahara et al., 2010). Given this situation, the increase in human occupations in Japan during late MIS 3, as indicated by the number of sites (Norton et al., 2010; Kudo and Kumon, 2013; Izuho and Kaifu, 2015) should not have been prompted by changes in biogeography in the Japanese Archipelago that would have “attracted” human foraging groups from continental East Asia. For instance, human foragers would not have been simply following large game to the islands given the absence of any land bridges. Rather, it may be possible that increasing human population density on the continent during MIS 3 (Wang, 2005; Bae and Bae, 2012; Bar-Yosef and Wang, 2012; Qu et al., 2013; Li et al., 2014; Lee et al., 2017) prompted humans to become more aggressive explorers to find new territories. Enhanced social networking and learning, notably advanced seafaring skills and shared knowledge of available resources in and around the exposed western part of the East China Sea may have facilitated large scale dispersals across the Tsushima Strait to Paleo-Honshu beginning during the latter part of MIS 3.

It is not clear whether a land bridge between Taiwan and the Ryukyus existed during the Late Pleistocene. The evidence for a land bridge at some point during the Middle Pleistocene seems more secure. For instance, based on the presence of *Mammuthus trogontherii* fossils, a land bridge connecting Taiwan, Ishigaki Island, and Miyako Island likely emerged during the late Middle Pleistocene (Kawamura et al., 2016). Because the specimen of *M. trogontherii* from the Tanabaru Cave in Miyako Island does not show dwarfism and is morphologically similar to a comparable Middle Pleistocene specimen from Taiwan, Kawamura et al. (2016) proposed that there was a land bridge between Taiwan, Ishigaki Island, and Miyako Island during a cold stage of the

late Middle Pleistocene, later than 0.45 Ma. No archaeological and human fossil records dated to the Middle Pleistocene have been found in the Ryukyus. Thus, it seems likely that the Ryukus were also initially peopled via watercraft some time during the Late Pleistocene (Nakagawa et al., 2010; Kaifu et al., 2015). Regardless of how the Ryukus were initially peopled, the recent mtDNA analysis on the Late Pleistocene human remains from the Shiraho-Saonetabaru Cave on Ishigaki Island in the Ryukyus identified B4e and M7a haplogoups, indicating a genetic connection between these humans and populations from mainland Southeast Asia (Shinoda and Adachi, 2017). Clearly, this suggests that there was at least some degree of gene flow during the Late Pleistocene between mainland Southeast Asia and the Ryukyu Islands.

At the opposite end of the Japanese archipelago, human dispersals from the continent to Hokkaido was viable from at least MIS 4 until the end of MIS 2 (71,000–11,500 years ago) through the land bridge along the Paleo-SHK Peninsula (Ono, 1990). Although only a very small number of archaeological sites attributed to MIS 4 and 3 in Hokkaido (e.g., Izuho et al., 2012) and Sakhalin (e.g., Vasilevski, 2003) have been identified, this may be due in part to sampling bias and a lack of reliable dates (Nakazawa and Yamada, 2015). However, given that the evidence of human occupation in Paleo-SHK only increases after ~26,800 years ago (Buvit et al., 2016), we expect earlier dispersals to the region to have been very minor in scale.

5. Discussion and conclusion

Despite the presence of clear land connections during MIS 16, 12, and 6, no evidence currently exists that early humans reached the Japanese archipelago during these periods. Based on current data, only via seafaring during MIS 3 did humans eventually arrive on the islands. Given these early foragers seafaring skills, it would not have been difficult to cross the Tsushima Strait during MIS 3, particularly because a great deal of evidence exists that obsidian was being moved, with some regularity, from Kozu Island off the Pacific coast of Paleo-Honshu to the Kanto Plain (e.g., Norton and Jin, 2009; Tsutsumi, 2010; Ikeya, 2015; Bae, 2017; Shimada et al., 2017).

Interestingly, during MIS 3, extinct proboscideans (i.e., *Palaeoloxodon naumanni*) and moose (*Alces alces*) were able to cross the Tsugaru Strait from Paleo-Honshu to Paleo-SHK (Hokkaido) (Takahashi et al., 2006; Fossil Mammal Research Group for Nojiri-ko Excavation, 2010). However, very limited evidence of a similar northward dispersal by human foragers around the same time appears to exist as comparative typological analyses of coeval Paleolithic stone tools from Honshu and Hokkaido indicate little relationship (e.g., Sakuma, 2017). Even assuming the advanced seafaring abilities these human foragers must have possessed, the reason why humans did not cross the narrow Tsugaru Strait (~20 km) to disperse from Paleo-Honshu to the southern Paleo-SHK Peninsula cannot be simply explained. It may be possible that some degree of biogeographic variation between Paleo-Honshu and Paleo-SHK Peninsula such as Blakiston's Line that separates the two regions across the Tsugaru Strait (Blakiston, 1883; Masuda, 1999, 2017; Hirata et al., 2013) could have lessened the human motivation to travel northward. Alternatively, the intrusion of the cold Oyashio Current from the Pacific Ocean to the Japan Sea after the LGM (Kido et al., 2007; Oba and Irino, 2012) and low degree of flow of the Tsushima Warm Current from the Japan Sea to Pacific Ocean due to the sea level drop, suggest variable oceanic currents may have influenced human dispersal patterns locally.

Pleistocene land bridges appear to have played little role in early hominin dispersals to the Japanese archipelago. The earliest peopling of the islands, thought to have occurred some time during MIS 3, is interesting because watercraft and advanced seafaring skills were almost surely involved. Given that these skills are traditionally assigned to modern humans, it would appear that only modern humans peopled these islands. Questions remain regarding the nature and timing of these dispersals to Paleo-Honshu and how they were similar or different from dispersals in the south to the Ryukus and in the north to Paleo-HSK.

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